COMPARISON OF THE MORPHOLOGY, FLOWERING PHENOLOGY, AND LIFE CYCLE TYPE IN PLANTS OF *GRINDELIA LANCEOLATA* (ASTERACEAE) FROM CEDAR GLADES IN MIDDLE TENNESSEE AND NORTHERN ALABAMA: A COMMON GARDEN STUDY

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ABSTRACT

The life cycle type of *Grindelia lanceolata* Nutt. has been described as biennial, short-lived monocarpic perennial, and (polycarpic) perennial in the taxonomic literature. Plants of this species in middle Tennessee cedar glades clearly are monocarpic. However, field observations suggested that those from glades in northern Alabama are at least dicarpic, and further that they differ morphologically and flower later than those in Tennessee glades. The purpose of this study was to determine if differences in morphology, flowering phenology, and/or life cycle type of Tennessee and Alabama plants are retained when grown from seeds in a "common garden" - i.e., in a nonheated greenhouse in Lexington, Kentucky. Morphological differences (all statistically significant) between *G. lanceolata* plants from Tennessee and Alabama were measure in the following: (1) size of both rosette and stem leaves; (2) number of secondary basal stems; (3) height of primary stem; (4) number of capitula per plant; (5) number of ray and of disk flowers per capitulum; (6) diameter of capitulum; and (7) length of ray flower corolla . Tennessee plants began flowering about 1 month earlier than Alabama plants, and none of them produced basal rosettes after they flowered once (in their 2nd year), confirming that they are strictly monocarpic. Alabama plants also flowered first in their 2nd year; however, 66% of them have produced basal rosettes (which bolted and flowered) for five consecutive growing seasons, confirming that they are polycarpic. Also, individual Tennessee plants potentially can produce twice as many seeds as individual Alabama plants during a single flowering/fruiting period. These results strongly suggest genetic differences exist in vegetative and floral morphology, flowering phenology, and life cycle type between Tennessee and Alabama plants of *G. lanceolata*. We speculate that these differences could be associated with different ancestral geographic origins: Tennessee plants from a monocarpic race in the Ozarks and Alabama plants from a perennial race in the Southwest.

RESUMEN

El tipo de ciclo de vida de *Grindelia lanceolata* Nutt. ha sido descrito, en la literature taxonómica, como bianual, como perenne monocárpico de vida corta y como perenne (policárpico). Las plantas

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de esta especie presentes en claros calcáreos del área central de Tennessee son claramente monocárpicas. Sin embargo, observaciones de campo sugieren que aquellas de la zona norte de Alabama son, al menos, dicárpicas; y mas allá, que difieren morfológicamente y que florecen más tarde que aquellas de los claros calcáreos de Tennesssee. El propósito de este estudio fue determinar si las diferencias en morfología, fenología floral y/o tipo de ciclo de vida de plantas de Tennessee y Alabama se mantienen cuando las plantas crecen a partir se semillas en un "jardin comun" - i.e., en un vivero sin calefacción en Lexington, Kentucky. Las diferencias morfológicas (todas estadísticamente significativas) entre plantas de *G. lanceolata* de Tennessee y de Alabama incluyen: (1) el tamaño de ambas clases de hojas, de roseta y de tallos; (2) número de tallos basales secundarios; (3) altura del tallo principal; (4) número de capítulos por planta; (5) número de flores radiales y de disco por capítulo; (6) diámetro del capítulo; y (7) longitud de la corolla de las flores radiales. Las plantas de Tennessee comenzaron a florecer aproximadamente 1 mes más temprano que las plantas de Alabama y ninguna de ellas produjo rosetas basales después de haber florecido una vez (en su 2do año), confirmando que son monocárpicas estrictas. Las plantas de Alabama también florecieron en su 2do año; sin embargo, 66% de ellas siguió produciendo rosetas basales (que desarrollaron tallo y florecieron) por cinco períodos de crecimiento, confirmando que son policárpicas. Además, cada individuo de Tennessee puede producir potencialmente el doble se semillas que los individuos de Alabama durante cada período de floración/fructificación. Los resultados sugieren claramente que hay diferencias genéticas en la morfología vegetativa y floral, la fenología floral, y los tipos de ciclo de vida entre plantas de *G. lanceolata* de Tennessee y de Alabama. Especulamos que estas diferencias pueden deberse a que estos dos grupos tengan diferentes orígenes geográficos: las plantas de Tennessee, de una raza monocárpica en los Ozarks; y las plantas de Alabama, de razas perennes del sudoeste.

INTRODUCTION

Grindelia lanceolata Nutt. (Asteraceae) is an herbaceous species that grows in open habitats on shallow soils underlain by limestone (Steyermark 1934, 1937; Baskin and Baskin 1979). Its geographical range extends from the Ozarks of Missouri and southeastern Kansas, south through eastern Oklahoma and northern and western Arkansas, and into northeastern and central Texas (Steyermark 1934, 1999; Correll and Johnston 1970; GPFA 1986; Smith 1988; Nesom 1990). Nesom (1990) also reports the species from the Monterrey area in Nuevo Leon, Mexico. Disjunct populations occur in the Central Basin of Tennessee (Chester et al. 1997) and in northern Alabama (Small 1933; Harper 1944), where they are associated closely with open cedar glades (Baskin & Baskin 1979, 1996; Baskin et al. 1995). *Grindelia lanceolata* has been reported from Louisiana (Rydberg 1932; Small 1933); however, Gandhi and Thomas (1989) do not list the species in their recent treatment of the Asteraceae of Louisiana. The species also has been reported from a single county in southeastern Ohio (Jones 1943; Fisher 1988), where, apparently, it has been introduced (Porter 1956).

In his taxonomic treatment of Texas species of *Grindelia*, Nesom (1990) recognized three varieties of *G. lanceolata*: *lanceolata*, *texana* (Scheele) Shinners, and *greenei* (Steyermark) Nesom, the latter known only from Mexico. However, Correll and Johnston (1970) did not recognize any separate taxonomic entities and thus included only *G. lanceolata* in their treatment. Julian A. Steyermark listed two forms of *G. lanceolata* in his Flora of Missouri (1999): *lanceolata* and *latifolia* Steyerm., the latter known from only one county in Missouri. Small (1933), Fernald (1950), Gleason (1963), GPFA (1986), Gleason and Cronquist (1991), and Chester et al. (1997) do not recognize any intraspecific taxa in *G. lanceolata*.

With regard to life cycle type, *G. lanceolata* has been reported to be biennial (Rydberg 1932), short-lived monocarpic perennial (Baskin & Baskin 1979; GPFA 1986; Gleason & Cronquist 1991), and (presumably polycarpic) perennial (Small 1933; Correll and Johnston 1970; Enquist 1987; Nesom 1990). In their study on the autecology and population biology of *G. lanceolata* in the limestone cedar glades of the Central Basin of Tennessee, Baskin and Baskin (1979) found that plants were short-lived monocarpic perennials (i.e., plants lived for a few years before they bolted and flowered once, and then died). The youngest plants to flower in the Baskins' study were in their third growing season (2+ years old). Other plants in the study flowered in their fourth or fifth year; all plants died after flowering once (i.e., monocarpic).

However, during field studies in the limestone cedar glades in northern Alabama, Baskin and Baskin (pers. obs.) noticed that Alabama plants of *G. lanceolata* differed in morphology, flowering time, and life cycle type. In contrast to plants in Tennessee, rosettes were present on those with dead flowering stalks in Alabama, suggesting that this species is at least dicarpic in the cedar glades of northern Alabama. The purpose of this study was to determine if there are distinct measurable or observable differences in vegetative morphology, floral morphology, flowering phenology, and/or life cycle type between *G. lanceolata* plants from Tennessee and Alabama cedar glades. To determine if differences in morphology and life cycle type are genetically—or environmentally—based, both Tennessee and Alabama plants were grown from seed in a common environment, i.e., a common garden experiment.

MATERIALS AND METHODS

Growth Conditions

All plants used in this study were grown from seeds in a nonheated greenhouse in Lexington, KY. Seeds were collected in autumn 1996 from *G. lanceolata* populations growing in cedar glades in Tennessee and Alabama and sown (separately) on soil in metal flats. The greenhouse soil mix was a 3:1 (v/v) mixture of limestone-derived topsoil and river sand. Following germination, juveniles were transplanted to 15-cm-diameter plastic pots in spring 1997 and assigned a number. Morphological and life cycle features of 103 Alabama plants and of 88 Tennessee plants were monitored in this study; plants of both groups were numbered consecutively.

Temperatures in the nonheated greenhouse were recorded continuously with an electric thermograph for the duration of the five-year study period. From these recordings, mean daily maximum and minimum temperatures for

TABLE 1. Five-year mean monthly maximum (± SE) and minimum (± SE) temperatures (°C) to which *Grindelia lanceolata* plants were exposed during the study.

Month	Maximum	Minimum
January	6.95 ± 1.4	1.71 ± 0.38
February	10.95 ± 0.88	4.00 ± 0.72
March	14.48 ± 1.40	5.65 ± 1.10
April	21.92 ± 1.30	11.81 ± 0.64
May	28.6 ± 0.77	18.22 ± 0.79
June	30.62 ± 0.46	20.9 ± 0.49
July	32.13 ± 1.20	23.15 ± 0.85
August	31.68 ± 0.92	22.05 ± 0.71
September	28.18 ± 0.95	17.75 ± 0.99
October	20.05 ± 0.35	12.6 ± 0.68
November	15.6 ± 1.10	8.23 ± 1.00
December	8.5 ± 1.40	3.03 ± 0.60

each month for each of the five years were determined. These temperatures then were used to calculate mean maximum (± SE) and minimum (±SE) monthly temperatures (°C) for the study (Table 1). Average daily photosynthetic photon irradiance at plant level in the nonheated greenhouse, measured with a LI-COR model LI-1000 data logger and three LI-190-SA quantum sensors, ranged from 6 mol m^{-2} d^{-1} on overcast days to 25 mol m^{-2} d^{-1} on clear days during the growing season (March to October) (Snyder et al. 1994).

Vegetative and Floral Morphology

To determine if there are differences in vegetative morphology, various leaf characters were compared between the two groups of plants. Length, width, oven-dry mass, and specific leaf area were determined for leaves collected from the rosette and from the lower-, middle-, and upper (just below the terminal capitulum) portions of the main stem. One leaf each from these four regions of the shoot was removed and measured/weighed for every plant in the study. Leaf length and width were measured to the nearest mm using a standard metric ruler. The width measurement was taken at the widest part of the leaf. Leaves were dried in an oven at 70°C for 24 hours, and their dry mass determined with an analytical balance. Average values for each leaf character were calculated for all plants in the study. Leaf prints were made using Diazo-type paper for ammonia developing, and leaf area (one side of leaf) was determined by weight of paper/area print relationships. Specific leaf area (SLA) was calculated using the following equation: $SLA = A_{leaf}/W_{leaf}$ where A_{leaf} is leaf area (one side only) and W_{leaf} is leaf dry weight. SLA was determined for one leaf from each of the four shoot levels for each plant in the study, and then average values were calculated for leaves of each position. In addition, number of secondary basal stems and height of each plant were determined and averages calculated. All means were compared by t-tests (P=0.05).

Number of capitula for the main stem and for all secondary stems were counted and averages calculated for each plant in the study. Floral measurements were made on 15 Tennessee plants and on 15 Alabama plants selected randomly using a random-numbers table. Number of ray and disk flowers, length and width of ray flower corolla, and diameter were measured, to the nearest mm, for the terminal capitulum of the main stem of each of the 30 plants. The terminal capitulum is always the first to flower on a plant. Capitulum diameter and corolla length and width were measured using a standard metric ruler and means calculated. All means were compared by t-tests (P=0.05).

Flowering Phenology

The terminal capitula of the main stems were monitored for flowering. The flowering period in this study extended from the beginning of flowering (indicated by the first anther of the first disk flower to shed pollen; ray flowers are pistillate) in the first plant and ended with the beginning of flowering in the last plant. Beginning of pollen shed was determined by brushing a finger across the anthers and observing if clumps of the bright yellow pollen adhered to it.

Seed Production Potential

To assess the reproductive effort of *G. lanceolata*, potential number of seeds per individual plant was calculated. Potential number of seeds per individual for Alabama and for Tennessee plants was calculated as follows: Potential number of seeds produced per plant = (Avg. no. capitula per main stem x Avg. no. ray flowers per capitulum) + (Avg. no. capitula per main stem x Avg. no. disk flowers per capitulum) + (Avg. no. capitula per secondary stem x Avg. no. secondary stems x Avg. no. ray flowers per capitulum) + (Avg. no. capitula per secondary stem x Avg. no. secondary stems x Avg. no. disk flowers per capitulum).

RESULTS

Vegetative and Floral Morphology

Length, width, dry weight, and SLA of leaves from the rosette, and from the lower-, middle-, and upper portions of the main stem, differed significantly between Tennessee and Alabama plants of *G. lanceolata* (Table 2). Only rosette dry weight and length of leaves on the lower portion of the stem were nonsignificant. In general, plants from Alabama had longer, wider, and heavier leaves, a higher SLA, and were taller than Tennessee plants. However, Tennessee plants produced significantly more secondary stems than Alabama plants (Table 2).

Tennessee plants produced significantly more capitula per plant on both main stems and secondary, basal stems than did Alabama plants (Table 3). Average number of capitula per main stem and per secondary stem was significantly higher for Tennessee plants. Alabama plants produced larger capitula

TABLE 2. Comparison (mean ± SE) of several vegetative and floral morphological characteristics of *Grindelia lanceolata* plants from Tennessee and Alabama. An asterisk indicates means for a character are significantly different (t test, P = 0.05), whereas NS indicates that they are not significantly different at this level.

Character	Tennessee	Signif. Level	Alabama
Rosette Leaf			
Length (cm)	8.6 ± 0.2	*	7.3 ± 0.2
Width (cm)	0.7 ± 0.01	*	0.9 ± 0.02
Weight (g)	0.038 ± 0.006	NS	0.045 ± 0.003
SLA (cm^2/g)	159.81 ± 11	*	211.37 ± 14
Lower Leaf			
Length (cm)	9.3 ± 0.1	NS	9.6 ± 0.2
Width (cm)	0.7 ± 0.2	*	1.2 ± 0.3
Weight (g)	0.039 ± 0.007	*	0.063 ± 0.006
SLA (cm^2/g)	173.53 ± 15	*	200.97 ± 7
Middle Leaf			
Length (cm)	7.8 ± 0.2	*	8.9 ± 0.2
Width (cm)	0.6 ± 0.01	*	1.3 ± 0.02
Weight (g)	0.031 ± 0.005	*	0.070 ± 0.002
SLA (cm^2/g)	115.84 ± 7	*	147.46 ± 14
Upper Leaf			
Length (cm)	6.3 ± 0.1	*	7.0 ± 0.2
Width (cm)	0.5 ± 0.02	*	1.0 ± 0.03
Weight (g)	0.0396 ± 0.002	*	0.057 ± 0.004
SLA (cm^2/g)	125.63 ± 5	*	135.86 ± 10
No. Secondary Stems	3.1 ± 0.2	*	1.4 ± 0.1
Height (cm)	55.39 ± 0.2	*	86.09 ± 0.2
Ray Flower Petals			
Length (cm)	1.45 ± 0.1	*	2.05 ± 0.3
Width (cm)	0.33 ± 0.06	NS	0.30 ± 0.04

(i.e., greater diameter) and more ray flowers per capitulum than did Tennessee plants. Number of disk flowers, however, did not differ significantly between the two groups. Ray flowers from Alabama plants had longer petals than Tennessee plants, but there was no difference in petal width between the two groups.

Flowering Phenology

All plants from both groups bolted and flowered in their second year. Flowering in Tennessee plants began on 1 July 1998, and all terminal flowers of main stems had flowered by 5 August 1998 (Fig. 1). In contrast, flowering in Alabama plants began and ended on 26 July and 7 September, respectively. For both groups, capitula elsewhere on the main stem and on secondary stems continued to

Table 3. Comparison of number of capitula and of ray and disk flowers produced by *Grindelia lanceolata* plants from Tennessee and Alabama. All values are expressed as means (± SE) except for total number of capitula produced by all plants. An asterisk indicates means of each character are significantly different (t test, P = 0.05), whereas NS indicates that they are not significantly different at this level.

Character	Tennessee	Signif. Level	Alabama
Total No. Capitula Produced			
Main Stem	629		408
Secondary Stems	271		53
No. Capitula Produced			
Main Stem	7.3 ± 3	*	4.0 ± 1
Secondary Stems	2.2 ± 0.5	*	1.1 ± 0.3
No. Ray Flowers	22 ± 4	*	31 ± 3
No. Disk Flowers	203 ± 34	NS	252 ± 71
Capitulum Diameter (cm)	4.4 ± 0.2	*	5.7 ± 0.5

flower 1–2 weeks following the beginning of anthesis of the last terminal main stem capitulum.

After completion of flowering, all Tennessee plants (n=88) died; not a single one produced a new basal rosette. However, many Alabama plants continued to produce new rosettes and to bolt and flower over the course of the five-year study period (Figs. 1, 2). One-hundred and three Alabama plants bolted and flowered in 1998, 78 in 1999, 74 in 2000, 73 in 2001, and 68 in 2002 (Fig. 2). Flowering period duration was 43 days in 1998, 48 in 1999, 43 in 2000, 39 in 2001, and 44 in 2002 (Fig. 1). Length of flowering period in 1998 was 36 days for Tennessee plants (Fig. 1). Flowering (both terminal and all other capitula) for both groups had been completed by mid-September.

Seed Production Potential

An individual Tennessee plant had the potential to produce an average of 3,128 seeds, while a single Alabama plant had the potential to produce only 1,568 seeds.

DISCUSSION

Observations by Baskin and Baskin that Alabama *G. lanceolata* plants appeared to be distinct in morphology, flowering time, and life cycle type from those in Tennessee were supported by the results of this study. Alabama plants are taller and have larger leaves than Tennessee plants. One of the more striking differences between the two groups is the number of secondary basal stems. Tennessee plants produce more than two times as many secondary basal stems as do Alabama plants, giving them a suffrutescent-like appearance. Indeed, Tennessee

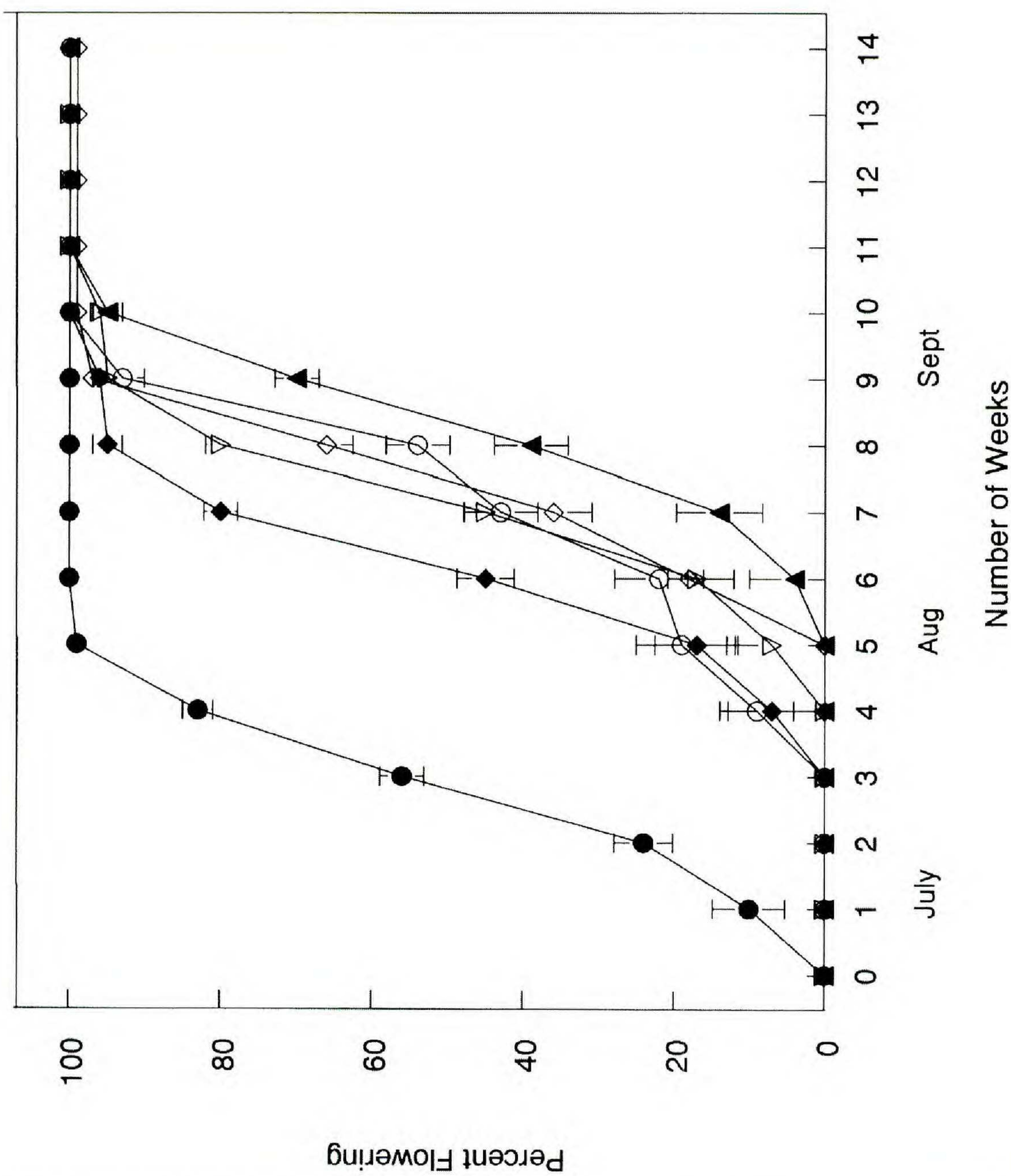

Fig. 1. Flowering phenology for 88 Tennessee *Grindelia lanceolata* plants in 1998 (●) and for 103 *Grindelia lanceolata* Alabama plants in 1998 (◆), 1999 (◇), 2000 ( ), 2001 (▲), and 2002 (○).

and Alabama plants can be distinguished easily on the basis of height and branching pattern.

Average diameter of the terminal capitulum of Alabama plants is greater, by more than 1 cm, than that of Tennessee plants. Compared to Tennessee plants, terminal capitula of Alabama plants produce significantly more ray flowers and longer ray petals. On the other hand, Tennessee plants produce twice as many capitula per secondary stem and nearly twice as many (1.85:1) per main stem as do Alabama plants.

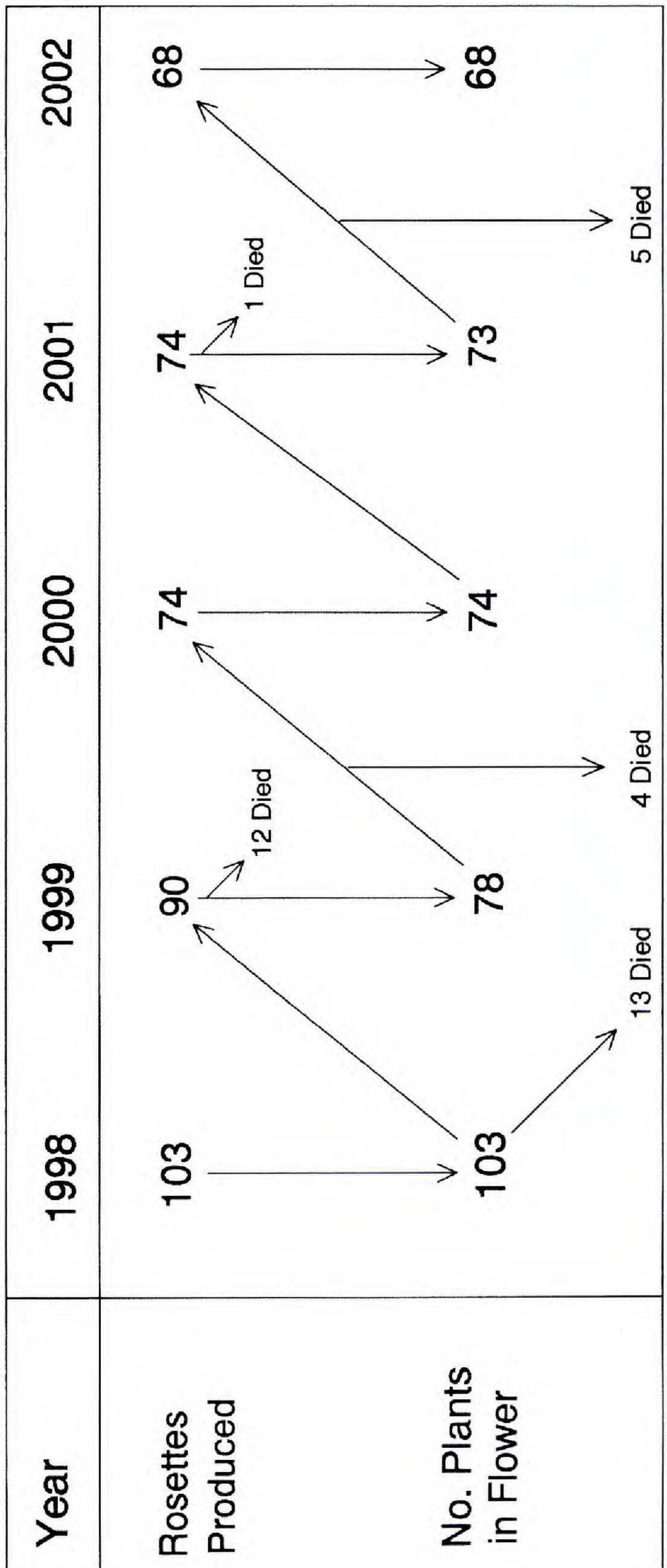

Fig. 2. Fate of 103 Alabama *Grindelia lanceolata* plants grown from seed in a non-heated greenhouse. All plants that produced rosettes in 1998 were in their second year of growth.

Number of seeds per plant produced during a single reproductive event was considerably higher in the monocarpic perennial ("biennial") plants (Tennessee) than in the polycarpic plants (Alabama). Salisbury (1942) reported that biennials in Great Britain produced an average of more than four times as many seeds as did polycarpic perennials. Duffy et al. (1999) predicted that monocarpic species should maximize the number of meristems (i.e., branches) devoted to reproduction, which would allocate as many reserves as possible to reproductive effort since there is only one reproductive event. Conversely, they predicted that polycarpic perennials should maximize the number of growth meristems (but not reproductive ones) since there is a fitness premium on longevity and competitive ability. Tennessee plants produced 2.2 times as many secondary basal stems, all of which flowered, as did Alabama plants. As a result, Tennessee plants produced, on average, significantly more capitula and had the potential to produce almost twice as many seeds as did Alabama plants. Thus, Tennessee plants obviously devoted more energy to reproductive meristems than did Alabama plants, which devoted more energy to growth in height and perennation. Whereas all Tennessee plants died after flowering once, the majority of Alabama plants continued to flower each year for several years. By producing fewer flowers, Alabama plants have reserve energy for production of new rosettes (i.e., perennation), which also should be considered growth meristems. Thus, there is a tradeoff between number of seeds produced per reproductive event and lifespan of an individual.

A very interesting difference between Tennessee and Alabama plants is life cycle type. In the nonheated greenhouse, both Tennessee and Alabama plants bolted and flowered in their second year. However, whereas all 88 Tennessee plants died after they reproduced once, only 13 of 103 Alabama plants did so. Thus, 100% of the Tennessee plants, but only 13% of the Alabama plants, behaved as biennials. Another 12% of the Alabama plants were dicarpic, 12% were tricarpic, and 1% tetracarpic, dying after their third, fourth, and fifth years, respectively. Sixty-six percent of the original 103 Alabama plants have flowered in their second, third, fourth, fifth, and sixth years, and it is expected that most of them could survive and flower for the next several growing seasons.

Apparently, differences in morphology, flowering time, and life cycle type between Tennessee and Alabama plants are genetically-based, since they were maintained in plants grown from seeds in a common environment. However, the advantage, if any, for *G. lanceolata* behaving as a short-lived monocarpic perennial in Tennessee glades, and of it behaving as a polycarpic perennial in the cedar glades in northern Alabama, is not known. Floristically and vegetationally, cedar glades of northern Alabama are very similar to those in central Tennessee (Baskin et al. 1995; Baskin & Baskin 1999, in press). Further, soils in both areas are limestone-derived, and climatic differences are minimal;

both areas are within Köppen's Cfa climate type (i.e., mild temperate rainy climate without a distinct dry season, and with a hot summer) (Ackerman 1941). Soil moisture and microclimate in cedar glades cause stress in plants in Tennessee glades (Baskin & Baskin 1999), and one would expect the same conditions in glades in Alabama. Thus, there are no apparent physical or biotic differences between Tennessee and Alabama glades that would seem to favor a monocarpic life cycle in one area and polycarpic life cycle in the other. A reciprocal transplant study would help to determine if, in fact, plants are subjected to different sets of selective factors on life history in the two areas, one favoring monocarpy and the other polycarpy.

In terms of r and K life history strategy (e.g., Pianka 1970), data collected in this study indicate that Tennessee plants are more r-selected than are Alabama plants, which are somewhat further along the r-K continuum to being K-selected. Thus, compared to Alabama plants, Tennessee plants are monocarpic, short-lived, smaller in stature, and much more productive in terms of numbers of seeds per reproductive event.

Could differences in geographic origin of Tennessee and Alabama plants account for the differences between them? Plants in Alabama glades could be disjunct from ancestor populations in southwestern United States, specifically in Texas. Texas floras (Correll & Johnston 1970; Enquist 1987; Nesom 1990) consistently describe the species as a (presumably polycarpic) perennial. This genetic race may have spread from Texas into Alabama, and the two groups became separated through geologic time. On the other hand, it seems likely that plants in the middle Tennessee cedar glades are disjunct from short-lived monocarpic or biennial races (Rydberg 1932; Wetter 1986; Gleason & Cronquist 1991) in the Ozark Region. Several other species, e.g., *Evolvulus nuttallianus* R. and S., *Oenothera macrocarpa* Nutt. subsp. *macrocarpa*, *Onosmodium molle* Michx. var. *subsetosum* (Mack. & Bush) Cronquist, and *Solidago gattingeri* Chapm. are disjunct between the limestone glades of Missouri and those in Tennessee, and none of these occurs in Alabama glades (Baskin & Baskin 1986; Bridges & Orzell 1986; Baskin et al. 1995; Baskin & Baskin in press).

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